

Decomposition and Nutrient Dynamics of Litter in Long-term Optimum Nutrition Experiments

I. Organic Matter Decomposition in *Picea abies* Needle Litter

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The chemical composition of the falling litter was investigated over the different fertilization regimes. The nitrogen concentration in the needle litter increased with dosage of nitrogen fertilizer. Nitrogen concentration in needle litter was positively correlated to those of lignin, sulfur and calcium, but negatively to those of zinc, aluminum, and manganese. Phosphorus concentrations were negatively correlated to those of lignin, manganese, zinc, calcium and magnesium. Concentrations of sulfur were negatively correlated to concentrations of zinc, calcium, aluminum, magnesium and boron. The decomposition patterns of Norway spruce needle litter were followed in an optimum nutrition field experiment. Control plots and plots given high dosages of nitrogen and phosphorus fertilizer were used. As decomposition proceeded soluble substances disappeared quickly and the concentration of soluble substances consequently decreased fast. Lignin, being a recalcitrant compound, increased in concentration and the concentrations increased linearly to accumulated mass loss. There was a clear difference in pattern as regards increase in lignin concentrations among needle litters depending on whether they were incubated in a control plot or a highly fertilized one. The concentration of lignin at a given mass-loss value was thus significantly higher for litter incubated in a fertilized plot than in the control plot. In late decomposition stages, mass-loss rates decreased linearly as compared to lignin concentrations among needle litters highly fertilized one. The concentration of lignin at a given mass-loss value was thus significantly higher for litter incubated in a fertilized plot than in the control plot. In late decomposition stages, mass-loss rates decreased linearly as compared to lignin concentrations, up to a certain concentration of lignin, after which some other factor was more rate regulating. No difference was seen between the control plot and the fertilized plot as regards the influence of lignin concentration on mass-loss rate. *Key words:* Norway spruce, needle litter, lignin, decomposition, nitrogen, phosphorus, nutrients, chemical composition.

INTRODUCTION

In many coniferous forests a harsh climate, acid soils and nutrient-poor, lignin-rich litter will contribute to the slow decomposition of coniferous litter (Berg & Staaf, 1980; Flanagan & Van Cleve, 1983). In undisturbed forest sites this will lead to an accumulation of organic matter in the forest floor, storage of essential nutrients, especially nitrogen, and probably phosphorus (Hesselman, 1937; Sire'n, 1955; Tamm & Carboneir, 1961) and thereby the eventual reduction of tree growth.

Among factors that influence the turn-over rate of the forest floor material, the chemical composition of the added tree litter has received some attention. In some studies, the

nitrogen concentration of the substrate was concluded to be the rate-limiting factor for litter decomposition (Melin, 1928; Kelly & Henderson, 1978; Edmonds, 1980).

In a study on decomposition of Scots pine needle litter, Berg & Staaf (1980) found that during the initial stages of decay the nitrogen and phosphorus concentrations had a strong positive relation to mass-loss rate, but as decomposition proceeded this effect disappeared. Lignin, which progressively was enriched in the litter, was suggested to gradually become the most influential substance and retard mass-loss rate. A similar development was reported by Pandey & Singh (1982) in a study on decomposing deciduous and coniferous tree litter in the Himalayas. They noted that, as decomposition proceeded, the relation between mass-loss rate and concentrations of nitrogen, calcium and water-soluble substances in the substrates weakened while the relation to lignin became stronger. For nutrient-enriched litter from nitrogen-fertilized Scots pines, Berg et al. (1987) found a strong retardation caused by lignin irrespective of nutrient level but when using leaf litters of a wider range of nutrient concentrations, Berg & Ekbohm (1991) could see that the decomposition rate of lignin in late stages of litter decomposition was inversely related to nitrogen concentrations, suggesting that also the decomposition rate of whole litter is being depressed by higher nitrogen concentrations.

In view of the frequent use of nitrogen fertilizer in forests the possible effects of fertilization on litter has a potential silvicultural interest, since fertilized trees produce a litter enriched in, e.g. nitrogen and phosphorus (Miller & Miller, 1976; Berg & Staaf, 1980).

With the selected site and substrate the decomposition process is almost entirely microbial (Persson et al., 1980). Needle litter also has a very low leachability (<1% of the mass could be leached initially).

The present study was part of a large project also investigating the effect of fertilization of Norway spruce and Scots pine on microclimate, especially ground climate and thereby on decomposition rates of soil organic matter. The study also included the effect on mass-loss rate of a changed chemical composition of the litter. The parts of the project dealing with microclimate and microclimate *versus* litter decomposition will be reported elsewhere. In this study we have investigated the decomposition of Norway spruce needle litter from stands given different doses of nitrogen and phosphorus fertilizer. We have had the following three aims, namely:

- to describe some chemical changes in Norway spruce needle litter during decomposition;
- to determine the influence of the litter's chemical composition on litter decomposition rate;
- to determine the influence of the litter's chemical composition on the net release rate of nutrients.

Of these, the two former aims are dealt with in the present paper whereas results concerning the third are presented in a report (Berg & Tamm, 1991) and in a later paper.

SITE DESCRIPTION

The site Stråsan, an optimum nutrition experiment, is located in central Sweden (60°55' N; 16°01' E) on a till soil. The site is located on a slope to the west, at a mean altitude of 350 m a.s.l. The annual mean temperature is +3.4°C (Vedin, 1973), and the annual precipitation 775 mm (Eriksson, 1980). Average AET is 422 mm (Eriksson, 1980).

The area was planted with Norway spruce (*Picea abies* L.) in 1958 and when the fertilization experiment started in 1967 the area was divided into plots measuring 30 m × 30 m. The dosages of nitrogen and phosphorus given to plots used are presented in Appendix 1. A detailed description of the experiment is given by Tamm et al. (1974). Tree growth development has been described by Tamm (1990).

MATERIALS AND METHODS

Needle collection, sample preparation, incubation and sampling

Norway spruce needle litters with different nutrient concentrations were sampled from an experimental Norway spruce forest, 24 years old (in 1982). Brown needle litter samples were taken in late summer (August), from trees in both control plots (NO) and plots given different doses of ammonium nitrate and/or a commercial preparation of phosphate (Appendices 1 and 2, and Table 1). The nitrogen fertilization had been performed as annual additions since 1967 (Tamm et al., 1974) whereas phosphorus had been added at three-to-four year intervals. Green needles were sampled from a control plot (NO) in early spring. In a special study on the variation of the litter's initial chemical composition, needle litter was sampled in late summer in two consecutive years (1983 and 1984). Needles were then shaken from branches of at least 10 trees in each plot of each of the treatments NO, N2 and N3 (Appendices 1 and 2).

The unified Scots pine needle litter was collected at the former site of the Swedish Coniferous Forest Project at Jädraås. Brown needles were collected from 25-year-old Scots pines in late September at the time for abscission. The needles were dried at room temperature and stored dry until the preparation of litter-bags took place. The trees were all located in an area of less than 100 m × 100 m.

Before weighing, the needles were air-dried at room temperature to about 5–8% moisture. Dry mass was determined at 85°C and the largest difference in moisture was less than 0.5 percentage units of the average ($n = 25$). The litter-bags measuring 10 cm × 10 cm were made of terylene net with a mesh size of 1 mm or 0.5 mm. Each litter bag enclosed an amount of about 0.7 g of needle litter (weighted with 3 decimals) and a piece of plastic tape giving the mass of the needles. The bags were fastened to the ground by 10-to-15 cm-long metal pins. Bags were incubated in the NO- and N2P2-stands only. In each of these stands, 25 random spots, each measuring 1 m × 1 m, were used for incubation of the litter bags.

Table 1. *Some chemical properties of needle litter from Norway spruce, collected at the nutrient optimum experiment Stråsan*

Sampling in 1980. Reference No is given to the set of litter in which each specific litter type was incubated in

Needle type	Concentration (mg.g ⁻¹)					
	Water solub. subst.	Ethanol solub. subst.	Lignin	N	P	Set No
Brown needles						
NO, b	101	60	340	4.2	0.41	1
NO, a	114	61	344	6.1	0.57	3
N1	147	45	334	7.1	0.42	2
N2	203	35	340	13.6	0.39	2
N3	158	29	340	18.3	0.26	2
P2	87	47	384	7.1	0.89	3
N2P2 a	302	47	242	4.5	0.75	2
N2P2 b	83	53	370	9.8	0.82	3
N2P1	68	48	407	9.4	0.72	3
Green needles						
NO	358	43	208	8.5	1.32	1

Norway spruce needle litter. Three different sets of needle litter were incubated and mass loss and chemical changes followed. Set 1 comprised brown and green Norway spruce needle litter from control plots. Incubation of both litter types were made in one NO plot and one N3P2-fertilized plot (cf. Table 1). The litter was incubated on June 30, 1982. Set 2 comprised brown spruce needle litter only. The 5 litter types originated from one NO plot and from plots given different dosages of fertilizer (cf. Table 1). The incubation of all litter types was made in one NO plot and one N2P2-fertilizer plot on Sept. 6, 1982. Set 3 comprised brown spruce needle litter only and the four litter types originated from one control plot and from plots given different dosages of fertilizer. The incubation was made on Sept. 12, 1983.

Unified Scots pine needle litter. In addition to the above incubations, needle litter of a unified Scots pine needle litter preparation was incubated in both control plots and in both N2P2 plots. These incubations were made twice annually starting on May 17, 1983 and took place in all seven times. Samplings were made about 3 to 4 times annually. The more exact sampling intervals and basic data are presented by Berg & Tamm (1991).

At each sampling one litter-bag from each of 25 incubation spots in each plot was collected. The litter-bags were transported directly to the laboratory and cleaned of moss, grass and dwarf-shrub remnants. After drying at 85°C they were weighed individually and then pooled to one sample and milled to pass a 1 mm screen before the chemical analyses were carried out.

Addition of fertilizer

During the incubation period fertilizer was added annually. The fertilizer was spread by hand to cover the experimental plot as evenly as possible. The litter-bags were not covered or protected but received fertilizer treatment too.

Chemical analysis

The amounts of water-soluble and ethanol-soluble substances were determined by ultrasonic treatment of the milled sample three times for each solvent in an ultrasonic bath and weighing the samples after filtration and drying. The analyses for sulfuric-acid lignin were carried out according to Bethge et al. (1971) (see also Berg et al., 1982).

The milled samples were also analyzed for total contents of the elements given below. Nitrogen was determined in an elemental analysis by combustion (Elemental Analyzer NA 1 500; Carlo Erba, Strumentazione 20 090 Rodano, Milan, Italy). For analysis of P, S, K, Ca, Mg, Mn, Fe, Al, Zn, Cu, and B samples were digested for 2 days in a 2.5:1 (v/v) mixture of nitric and perchloric acid. The analyses were performed by plasma atomic emission spectrometry ICP-AES (Jobin YVON JY-70 Plus, 16–18, rue du Canal, F-91 163, Longjumeau, France). Ash concentration was determined by combustion at 550°C for 2 h.

Terminology

For convenience we have used the term “lignin” for sulfuric-acid lignin throughout the paper despite being aware that the term is not fully correct as the analytical method used may register not only other aromatic compounds formed during the decomposition process, e.g. humification products (Berg & Theander, 1984), but also part of the litter’s ash. However, Nordén & Berg (1989), using high-resolution ¹³C-NMR, found no qualitative difference in aromatic components in Scots pine needle litter decomposing from 0 to 73% accumulated mass loss, an observation that may support the use of this terminology.

For the sake of simplicity we also denominate the control plots NO and the plots given nitrogen, or phosphorus, or nitrogen plus phosphorus fertilizer N2, N3, P2, N2P1 and N2P2 plots (cf. Appendix 1).

Storage of basic data

All data on mass loss and chemical composition are stored in computer files and in reports (Berg et al., 1991 a; Berg & Tamm, 1991) and are available upon request.

RESULTS AND DISCUSSION

Initial chemical composition

There was a clear variation in chemical composition of needle litter between different fertilizer regimes (Table 1; Fig. 1; Appendix 2). We may see that the variation in water-soluble substances among the brown needles ranged from 68 to 302 mg g⁻¹. The concentrations of ethanol-soluble substances had a narrower range with 29 and 61 mg g⁻¹ as extreme values. No relation was seen between dosage of fertilizer and concentrations of these components. Concentrations of lignin varied too, and ranged from 242 to 407 mg g⁻¹. In this unsystematic collection of litter, intended for decomposition studies, no relation was seen between lignin and nitrogen concentrations in litter (cf. below). However, the concentrations of nitrogen appeared to be largely in proportion to the dosage of fertilizer, the range being from 4.2 mg g⁻¹ in NO (control) plots to 18.3 mg g⁻¹ in a high-dosage (N3) plot.

A negative relation between concentrations of phosphorus and those of nitrogen was seen. On the other hand, all plots given phosphorus fertilizer produced litter with relatively high phosphorus concentrations, even if no clear difference could be assessed between the P1 and P2 treatments. The fact that the spruce needles stay on the branches as dead for at least several months (H. Staaf, pers. comm.) probably means that a leaching may have taken place and that the decomposition of the needles had started. We may even expect that part of them will be in a late phase of decomposition when they fall (cf. Berg & Staaf, 1980). Thus, mainly the more recalcitrant organic-chemical compounds should be left in the needles.

In a special study on initial chemical composition of litters, samplings were made in all plots fertilized with three different levels of nitrogen, namely all NO ($n = 5$) all N2 ($n = 5$) and all N3 ($n = 5$) plots. Nitrogen was the only macronutrient the dosage of which was varied. In some of the plots additions of K and other micronutrients were made. One systematic sampling was made in each of the years 1983 and 1984. In both sets concentrations of lignin, ash and a range of nutrients viz. N, P, S, K, Ca, Mg, Mn, Al, Fe, Zn, Cu, and B were analysed for and possible linear relations were investigated for.

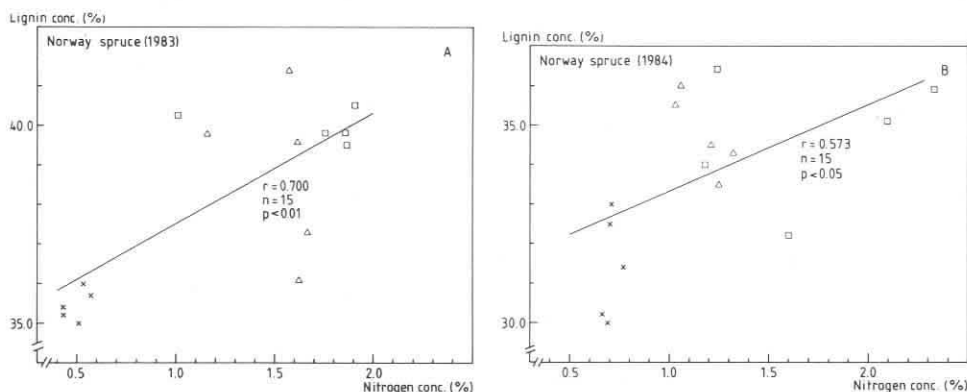


Fig. 1. Linear relations between nitrogen and lignin concentrations of Norway spruce needle litter. Collections were made in 1983 (left figure) and 1984 (right figure). NO plots (x), N2 plots (Δ) and N3 plots (□).

There were evident differences in chemical composition between both samplings, e.g. in concentrations of lignin, nitrogen and calcium (Appendix 2). Thus, with the evident between-year variation three different sets of regressions were run. We hypothesized that any secure correlation between components should be seen not only in both sets separately but also in the full set of data. Thus, three comparisons were made. In a first step, data for both years were combined and regressions made for the whole set. In a second step each sampling year was investigated separately and significant correlations were noted (Table 2).

In both of the years 1983 and 1984 there were some components that were well correlated. Ash is, of course an unspecific component and has been excluded from the more specific comparisons, but it deserves to be pointed out that there were negative correlations between dosage of nitrogen fertilizer and ash concentrations in the needle litter.

When all data were analyzed it appeared that there were several chemical components the concentration of which were correlated. The three main nutrients (nitrogen, phosphorus and sulfur) were correlated to several other nutrients and all of them were significantly correlated with calcium and zinc. Whereas there was a positive correlation between nitrogen and calcium the other relations between nitrogen and other nutrients were negative (Table 2). Both nitrogen and sulfur were, in addition, negatively correlated to aluminum, nitrogen alone negatively related to manganese. Sulfur was negatively correlated to boron and magnesium and phosphorus to magnesium. Calcium was well correlated negatively to manganese and zinc. Other nutrients that were correlated were manganese and zinc being correlated positively. Further, copper and aluminum concentrations were correlated with a negative relation and finally boron and iron concentrations with a positive relation. The positive correlation between calcium and zinc had an outstanding correlation coefficient of 0.954 when testing for the full set (Table 2). Correspondingly high r values were also found when each year was tested separately.

Decomposition patterns of the needles in unfertilized (NO) and fertilized (N2P2) plots

Organic-chemical changes. Some changes in organic-chemical composition were followed during the decomposition of the needles, namely the changes in the groups of water- and

Table 2. Correlation coefficients for linear correlations between concentrations of different nutrients and lignin in Norway spruce needle litter collected in control plots and plots given two levels (N2 and N3) of nitrogen fertilizer

The collections were made in the years 1983 and 1984 and the correlation coefficients given here are those obtained when the data for both samplings were combined.

Lignin	N	P	S	K	Ca	Mg	Mn	B	Cu	Al	Zn	Fe
Lignin	—											
N	+0.481	—										
P	−0.332	—										
S	+0.826		—									
K				—								
Ca	+0.738	−0.539	−0.531	−0.513	—							
Mg		−0.354	−0.387			—						
Mn	−0.382	−0.691			+0.760		—					
B			+0.363					—				
Cu						+0.351			—			
Al	+0.459	−0.521	−0.428						−0.586			
Zn	−0.761	−0.564	−0.592	−0.509	+0.954			+0.750		−0.518		
Fe									+0.716			

ethanol-soluble substances, as well as those for lignin (for nutrients dynamics, see Berg & Tamm, 1991). The concentration of lignin in litter increased with accumulated mass loss. This has been found earlier for a number of other litter types (Berg et al., 1984; Fogel & Cromack, 1977) and is simply an enrichment of a compound relatively recalcitrant to decomposition. This main pattern was seen in litter incubated both in the control (NO) and fertilized (N2P2-treated) plots. The concentrations of lignin as compared to accumulated mass loss increased linearly (Fig. 2a, set 1) and at 50% accumulated litter-mass loss the lignin concentrations had reached levels of around 500–520 mg g⁻¹ in the control plots (Appendix 3). The lignin concentration (as compared to accumulated mass loss) in a litter incubated in an N2P2 plot increased more quickly than that in a chemically identical litter incubated in a control plot. For brown needle litter the slopes were thus 2.71 and 3.51 when incubated in the control plot and the N2P2 plot respectively. When green nutrient-rich needle litter was compared the results were similar. The initial lignin concentrations were lower but the increase in lignin concentration in the fertilized plot was significantly higher

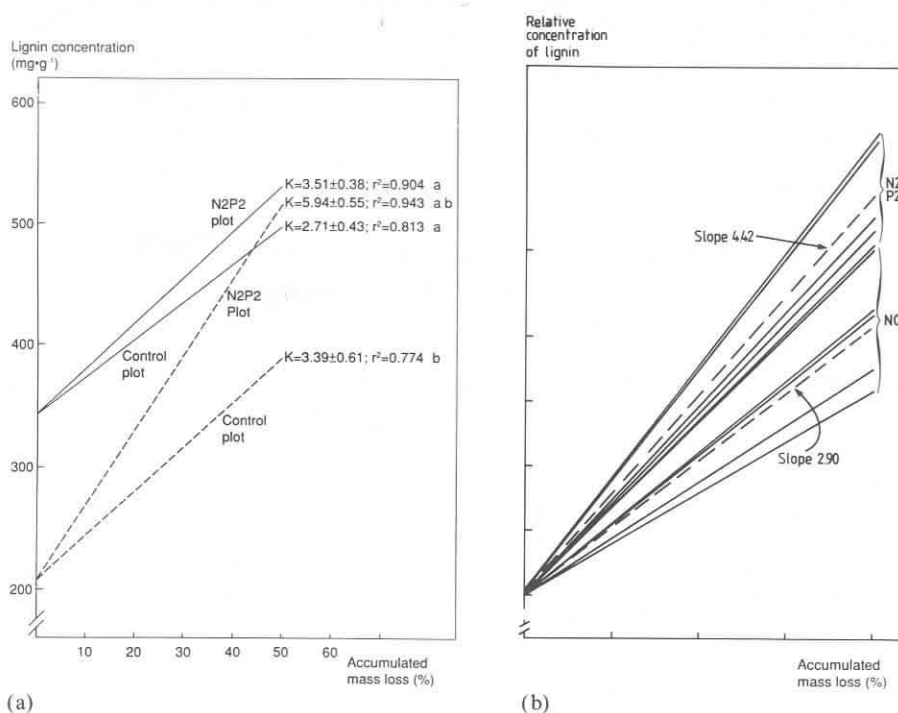


Fig. 2. Concentration of lignin in decomposing Norway spruce needle litter as compared to accumulated mass loss in; a. Litter of set No 1. Brown needle litter from a control plot incubated in a control plot (full line, $k = 2.709$) and an N2P2 plot (full line, $k = 3.390$). Green needle litter incubated in a control plot (dashed line, $k = 3.390$) and a fertilized one (dashed line, $k = 5.948$). Basic data for the regressions in Appendix 3. Lines indicated with the same letter are significantly different. b. Litter of set No 2. Five sets of needle litter incubated in the same control lot (NO) and the corresponding sets incubated in the same N2P2 plot. For the average slope in the N2P2 plots (4.42) the standard deviation was 0.51 and for the average slope of the control plots (2.9) it was 0.58. The difference between the averages was significant (t -test).

(slope 5.940) than in the litter incubated in the control plot (slope 3.390). A comparison was also made using set No 2 of incubated spruce needle litter (Fig. 2b) and the slopes for the equations of lignin concentration *versus* accumulated litter mass loss were compared. The slopes were calculated only in the interval where the increase was linear, in this case 0–40% accumulated mass loss. In all cases the linearity was highly significant. Upon a comparison of all the slopes it is easily seen that the average slope in the fertilized plot was about 1.5 times the average of that of the control plot with 4.42 (SD = 0.51) and 2.90 (SD = 0.58) for litter in fertilized plot and control plot respectively (Fig. 2b). This difference was highly significant ($p < 0.001$; t -test). The litter preparations used in this latter comparison had different initial concentrations of lignin among the five litter types used. However, chemically identical litters were incubated simultaneously in the two different treatments viz. the control plot and the fertilized plot. So in this comparison a given litter was incubated in both types of plots and it was also possible to make pairwise comparisons for each litter type resulting in that for each single litter type the slope was always higher in the fertilized plots.

This kind of observation, even if statistically significant, has no simple explanation. It is thus possible that a higher level of ammonium in the soil and litter may repress the degradation of lignin in the fertilized plot whereas a certain decomposition may take place in the NO plots thus giving a lower concentration. Such a relation, found by Kirk et al. (1976) for a fungal species, apparently is fairly general. This type of repression may take place to a certain level without a total stop in decomposition of litter. We did not, however, follow litter decomposition further than to about 50%. An alternative explanation is the incorporation (fixation) of ammonium/ammonia into the lignin remains which then turn into more recalcitrant compounds (cf. review by Nömmik & Vahtras, 1982). This kind of reaction may be limited by the amount of ammonia present (Axelsson & Berg, 1988) an observation which may explain, at least partly the strong increase in lignin concentration in N2P2 plots. If this explanation should hold, the effect of nitrogen on lignin concentration may be a more long-term one and may reveal itself more strongly in later decomposition stages of litter. It has also been observed (Söderström et al., 1983) that humus from heavily fertilized plots has much lower microbial biomass and respiration rates than that from unfertilized ones. The effect observed by them still lasted five years after the end of the fertilization.

One final possible explanation of this observation may be that there is a difference in microbial populations between the treatments, e.g. in proportions of active mycelium of the lignin-degrading brown-rot and white-rot fungi. This is in part supported by an investigation on the species of fruiting bodies in the two types of plots of the present study. There was a clearly significant difference in species composition and number of species (Agnetha Strandberg, pers. comm.), with the fertilized plots having relatively few species.

Rate regulating factors for the decomposition of spruce needle litter

Comments on the variability in decomposition rate and its relation to climatic factors. It appeared that the brown spruce needles in general were decomposed more slowly than were Scots pine needles in the same stand and time period (Table 3; cf. Berg & Tamm, 1991). Whereas the average value for first-year mass loss for Scots pine needles was 27.3% in control (NO) plots it was 22.8% for brown Norway spruce needles. This difference was significant. The significance was tested for, using t -test and 14 and 13 average mass-loss values respectively for the both litter types.

Upon a comparison between the NO and N2P2 plots using unified Scots pine needle litter in both plots it was found that the average decomposition value was significantly lower for the latter treatment (24.7% *versus* 27.3% in the NO plot), reflecting an average difference in the soil's temperature and moisture climate (cf. Jansson & Berg, 1985), which favoured a

Table 3. Average mass-loss values for the first year of decomposition of brown and green Norway spruce and brown Scots pine needle litters

Both mass-loss values of incubated litter sets and standard errors are given. Values within each column that are significantly different are indicated by different letters

	NO plots	First-year mass loss (%)			
		<i>n</i>	N2P2 plot	<i>n</i>	sign diff
Scots pine (brown)	27.3 (0.94) ^a	14	24.7 (0.83) ^a	14	$p < 0.001$
Norway spruce (brown)	22.8 (0.35) ^b	13	23.5 (0.40) ^a	9	n.s.
Norway spruce (green)	33.3 (—) ^c	1	31.6 (—) ^b	1	n.s.

higher mass-loss rate in the NO plots. When comparing the single mass-loss values for the two treatments in the same time period more clear patterns were seen (Berg & Tamm, 1991). A detailed comparison of soil climatic differences is presently being made (P.-E. Jansson, pers. comm.).

The unified Scots pine litter preparations have been used in earlier studies as a biological indicator of differences in the moisture and temperature climate of the soil (Jansson & Berg, 1985). The purpose of using this litter in the present study was to use chemically identical litter to be able to secure climate-dependent differences in decomposition rates between plots from those due to substrate quality.

For the brown spruce needles it was seen that decomposition rates were very similar on a one-year (first-year) basis in NO-and N2P2 plots (*t*-test; Table 3), in spite of the differences in ground climate. The reason for this similarity may be that the higher lignin concentrations of the litters had a rate-retarding effect, strong enough to dominate the difference in climate-dependent decomposition rate. This applied to all the sets of brown spruce needle litter incubated. The green spruce needles, which were rich in more readily decomposed compounds, e.g. water-soluble substances, showed a clear difference in mass-loss rates between NO and N2P2 plots (Fig. 3; basic data in Appendix 3).

Substrate quality factors. We may conclude that there was no measurable difference among the plots in mass-loss rate of brown Norway spruce needle litter caused by climatic differences. Therefore a comparison was made between annual mass loss and other rate-regulating factors, namely initial concentrations of nitrogen, phosphorus, water solubles, and lignin (Table 4).

There was no statistically significant relation between mass-loss rates in early decomposition stages and concentrations of nitrogen and phosphorus. It appeared, though, that the

Table 4. Correlation coefficients for the linear relation between Norway spruce needle litter mass loss and initial concentrations of nitrogen, phosphorus, water soluble substance and lignin

Time period (days)	N	Corr.coeff. P	W.S.	Lignin	<i>n</i>
254–261	0.285 (n.s.)	–0.609 (n.s.)	0.893 ($p < 0.01$)	–0.699 (n.s.)	8
361–365	0.003 (n.s.)	–0.188 (n.s.)	0.870 ($p < 0.01$)	–0.884 ($p < 0.01$)	9
728–772	0.547 (n.s.)	–0.762 (0.05)	0.952 ($p < 0.001$)	–0.620 (n.s.)	8

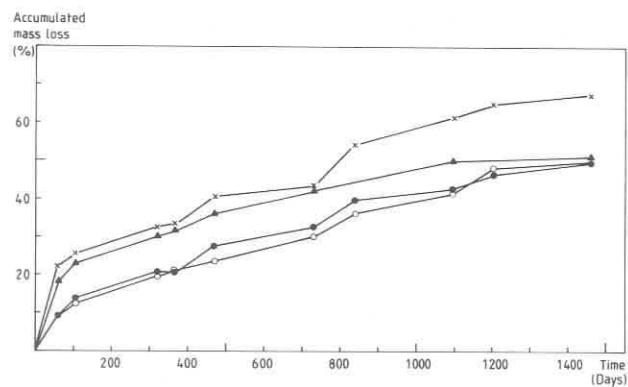


Fig. 3. Accumulated mass loss for green Norway spruce needle litter incubated in a control plot (x) and a fertilized one (▲). Brown Norway spruce needle litter was also incubated in a control plot (○) and in a fertilized one (●). Basic data in Appendix 3.

initial concentration of water solubles had a clear rate-increasing influence on initial mass-loss rate and on accumulated mass loss for about two years of decomposition (Fig. 4). The initial concentration of lignin which could be rate retarding had a less pronounced effect for the first year even if it was statistically significant. It thus appears that there was no nutrient-regulated early decomposition phase like that described by Berg & Staaf (1980), but one based on water-soluble substances. The effect on decomposition rate caused by the water-solubles' fraction may be explained partly as stimulated co-metabolism (a priming effect) caused by more easily decomposed chemical compounds.

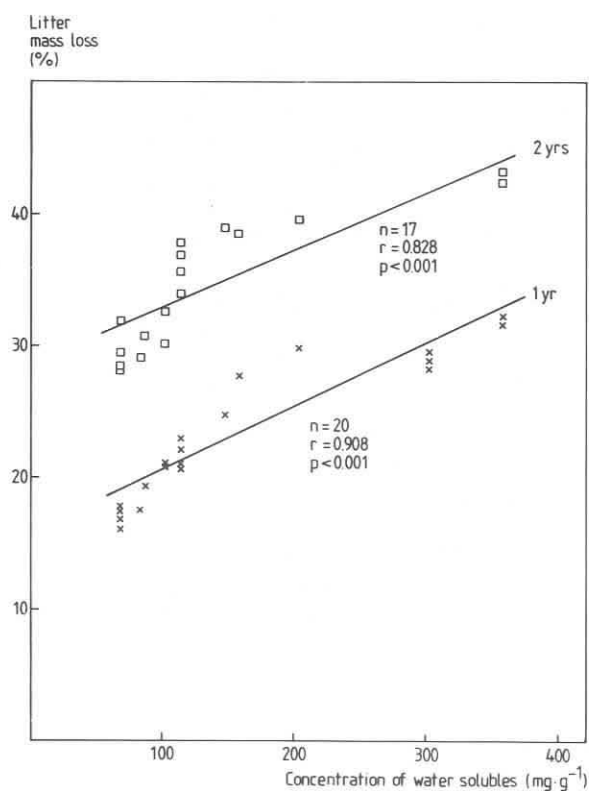


Fig. 4. Litter mass loss (Norway spruce needles) as dependent on the initial concentration of water-soluble substances. The relations are given for fertilized and control plots together. Accumulated mass loss after 1 yr. (x), and after 2 yrs (□).

Table 5. *Correlation coefficients for the linear relation between annual mass loss of Norway spruce needle litter and initial concentrations of lignin at the start of each one-year period*

Data from the two control plots (cf Fig. 5a).

	<i>r</i>	<i>n</i>	<i>p</i>	Denom. in Fig. 5a	Comment
1st incub yr	-0.894	10	<0.001	(1)	
2nd incub yr	-0.482	11	n.s.	(2)	
3rd incub yr	+0.234	11	n.s.	(3)	
4th incub yr	-0.376	8	n.s.	(4)	
Lignin conc. <450 mg · g ⁻¹	-0.875	16	<0.001		model stable also without the 3 low-lignin points
Lignin conc. <475	-0.774	22	<0.001		
Lignin conc. <500	-0.667	29	<0.001		

The possible rate-retarding influence of lignin concentration on mass-loss rate (cf. McClaugherty & Berg, 1987) was tested using mass-loss values for one-year decomposition periods and the lignin concentration at the start of each one-year period. The rate-retarding effect caused by lignin has been noted to start at raised lignin concentrations (e.g. Berg & Staaf, 1980). To be sure that the needle litters used were in a lignin-regulated decomposition phase, we decided to use only pairs of values for the regressions in which the lignin concentrations were higher than 300 mg g⁻¹. All decomposition values for spruce needle litter from the two NO (control) plots were used together whereas those from the two N2P2 (fertilized) plots were not included in the primary analysis. When thus comparing annual mass losses and lignin concentrations it appears that the concentration of lignin had a rate-retarding effect on litter decomposition—at least up to a certain value on the concentration of lignin (Table 5; Fig. 5a). It thus seemed that the simple rate-retarding effect of lignin lasted until a lignin concentration of about 450 mg g⁻¹. It was possible to distinguish a similar pattern in the N2P2 plots using all spruce needle litter decomposition data (Fig. 5b).

When comparing the effect of lignin concentration on litter mass-loss rate for separate incubation years it was noted that whereas in the first year there was a statistically significant relation there was none in years 2, 3, and 4 (Table 5). For the first year the relation also held, even if the three very low lignin values were excluded (Fig. 5a). In their study on rate-regulating factors in Scots pine needle litter, McClaugherty & Berg (1987) found that the rate-regulating effect of lignin is in effect up to a certain lignin concentration. As the increase in the concentration of lignin continues until it approaches an asymptotic (maximum) value the rate-regulating effect is exerted below this value. It also appears that the influence of some other component may take over when the lignin concentration approaches the value of the asymptote and does not increase further. Also Berg et al. (1987) noted this. The present study appears to generalize this finding and it is seen (Fig. 5) that above a lignin concentration of 500 mg g⁻¹ the variation in annual mass-loss values (as compared to lignin concentration) increased considerably, even if the linear relation still held (Table 5). In the marked interval (<450 mg g⁻¹) the decrease in decomposition rate was considerable and one may see that an increase in lignin concentration from 350 to 450 mg g⁻¹ caused a decrease in annual mass loss from 24 to 10% (Fig. 5a).

Data from both the NO (control) plots and the N2P2 plots were tested for in the same linear relation (Fig. 6). In this case we selected data from one plot of each type, namely the

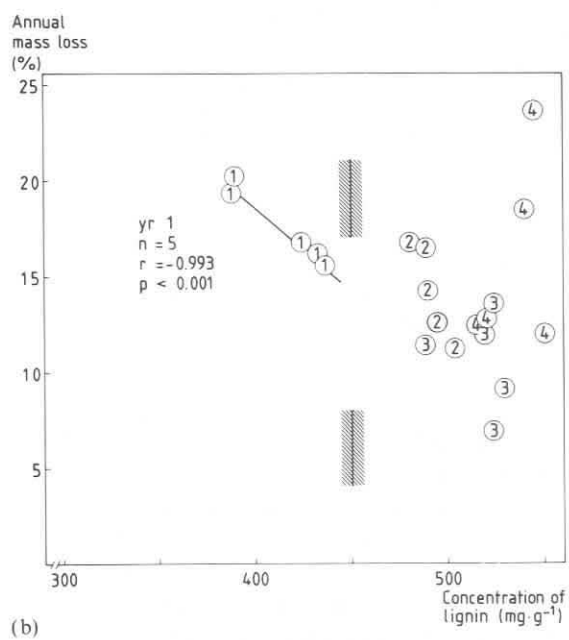
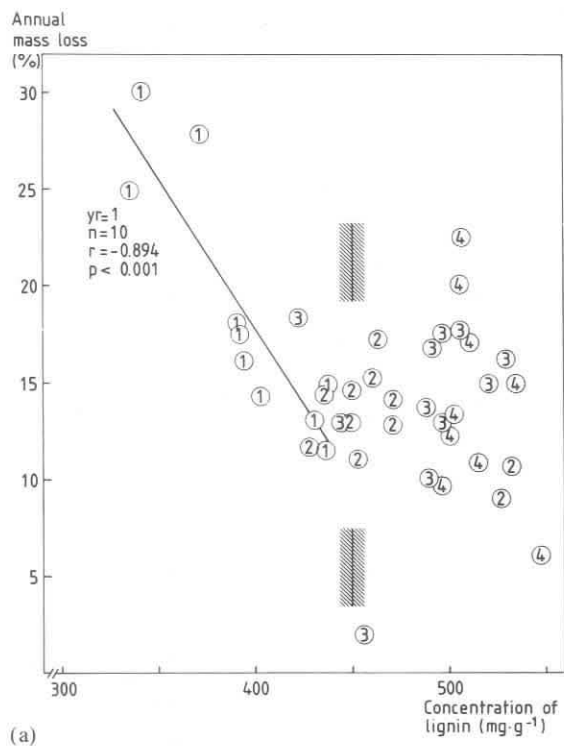


Fig. 5. Annual mass loss of Norway spruce needle litter as compared to lignin concentration in litter at the start of each one-year period. All values obtained from the two control plots were used (a) as well as all values from the two fertilized plots (b). The number in the circle gives the approximate incubation year.

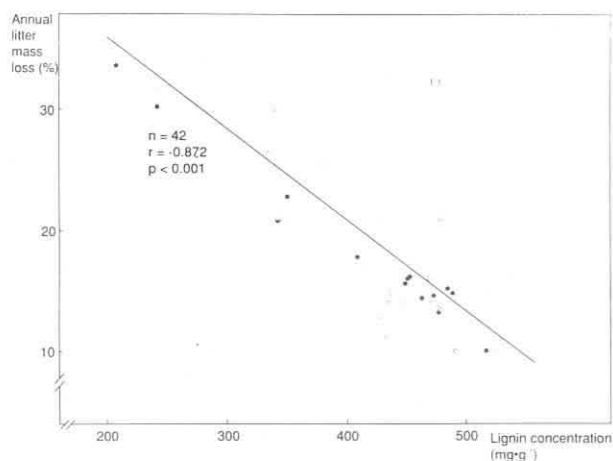


Fig. 6. Annual mass loss of Norway spruce needle litter in a control (○) and an N2P2 plot (●) as a function of lignin concentrations in the same time period. One odd value (within paranthesis) was not included in the linear regression and the *r*-value thus improved from -0.790 to -0.872.

control plot and the fertilized plot in one of the experimental blocks. The present Norway spruce system thus differed from some Scots pine systems where very different rate-regulating effects were obtained for litter incubated in control plots and in fertilized plots (cf. Berg et al., 1991 b)

CONCLUDING REMARKS

Lignin decomposition rate was observed to be rate determining (rate decreasing) for litter decomposition from the very early stages. The faster relative increase of lignin concentration in litter incubated in fertilized plots creates a more recalcitrant substrate faster than in non-fertilized plots. In spite of this, no effect was seen as regards lignin concentration on mass-loss rate. The effect observed in some forests where the accumulation of soil organic matter has been seen to take place at a markedly higher rate in fertilized forests than in undisturbed ones possibly is not general. One of two conditions for that to occur is that the humus in fertilized plots should be more recalcitrant to decomposition. This would be due not only to the relatively higher concentration of lignin but also to a higher nitrogen concentration (cf Berg & Ekbohm, 1991). Observations supporting this have been made in Scots pine forests but should not necessarily be connected to the tree species but could also depend on factors such as the ground's general nutrient status which is one of several factors that would determine the composition of the soil's microorganisms.

The concentration of water-soluble substances had a rate-enhancing influence on litter mass-loss rate in the early stages and the effect could be seen also when the litter had reached the late stages of decomposition. This observation may add to the conclusions above that fertilization of this type of system does not stimulate decomposition rates.

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Appendix 1. *Dosages of fertilizer given the plots used at the optimum nutrition experiment Stråsan.*

No additions were made to control plots. From Tamm et al., (1974) and Tamm, (1990). A dash indicates "no addition"

Year	Denomination of plot and addition (kg ha ⁻¹ yr ⁻¹)							
	P2	N1	N2	N3	N2P1	N2P2		
	P	N	N	N	N	P	N	P
1967	40	60	120	180	120	20	120	40
1968	–	60	120	180	120	–	120	–
1969	40	60	120	180	120	20	120	40
1970	20	40	80	120	80	10	80	20
1971	–	40	80	120	80	–	80	–
1972	–	40	80	120	80	–	80	–
1973	–	40	80	120	80	–	80	–
1974	40	40	80	120	80	20	80	40
1975	–	40	80	120	80	–	80	–
1976	–	40	80	120	80	–	80	–
1977	40	30	60	90	60	20	60	40
1978	–	30	60	90	60	–	60	–
1979	–	30	60	90	60	–	60	–
1980	40	30	60	90	60	20	60	40
1981	–	30	60	90	60	–	60	–
1982	–	30	60	90	60	–	60	–
1983	–	30	60	90	60	–	60	–
1984	40	30	60	90	60	20	60	40
1985	–	30	60	90	60	–	60	–
1986	–	30	60	90	60	–	60	–

About every fourth year an addition of boron was given the size varying between 600 and 2500 g ha⁻¹.

Appendix 2. Concentrations of soluble substances, lignin, nutrients and ash in Norway spruce needle litter collected at plots with three fertilization regimes (cf. Appendix 1) namely control (NO), N2 and N3

Samplings were made in 1983 and 1984. Average values are given and standard deviation within parenthesis. In all cases $n = 5$.

Year of sampling and type of needles	Concentration (mg g ⁻¹)								
	Water- soluble subst.	Ethanol soluble subst.	Lignin	N	P	S	K	Ca	Mg
1983									
NO	82.0	57.1	350	5.1	0.51	0.754	0.69	16.0	0.62
NO	90.7	47.9	360	5.3	0.48	0.714	0.88	11.5	0.51
NO	95.2	52.7	354	4.3	0.43	0.708	0.71	20.6	0.70
NO	90.9	53.1	352	4.3	0.42	0.756	0.66	20.8	0.72
NO	72.5	40.0	357	5.7	0.41	0.739	0.64	20.4	0.70
Mean	86.3	50.2	355	4.9	0.45	0.734	0.72	17.9	0.65
S.D.	9.1	6.5	4.0	0.6	0.04	0.022	0.10	4.08	0.09
N2	76.6	37.1	414	15.8	0.61	0.971	0.94	8.8	0.63
N2	96.7	36.1	373	16.6	0.49	0.988	1.25	12.5	1.04
N2	93.5	49.0	361	16.2	0.57	0.901	0.97	9.5	0.72
N2	80.2	31.6	396	16.2	0.52	0.391	1.06	9.7	0.75
N2	66.0	43.5	398	11.6	0.50	0.835	0.96	9.3	0.56
Mean	82.6	38.5	388	15.3	0.54	0.925	1.04	10.0	0.74
S.D.	12.6	7.4	21.2	2.1	0.05	0.061	0.13	1.5	0.18
N3	71.4	31.9	398	17.6	0.43	0.951	1.77	7.3	0.69
N3	62.4	30.8	398	18.6	0.48	0.971	1.20	9.2	0.83
N3	77.1	37.2	395	18.7	0.47	0.949	1.13	8.1	0.87
N3	63.4	30.7	405	19.1	0.61	1.126	1.64	7.7	0.82
N3	64.8	35.3	415	10.1	0.75	0.879	0.63	6.2	0.60
Mean	67.8	33.2	402	16.8	0.55	0.975	1.27	7.7	0.76
S.D.	6.3	2.9	8.0	3.8	0.13	0.091	0.45	1.20	0.11
1984									
NO	154.0	50.0	300	6.85	0.50	0.837	1.48	14.3	0.65
NO	152.0	52.7	319	6.55	0.47	0.727	1.60	13.0	0.73
NO	112.4	53.3	330	7.06	0.62	0.705	1.27	14.1	0.66
NO	106.5	45.7	314	7.67	0.66	0.724	1.22	13.0	0.54
NO	110.4	50.7	325	6.98	0.56	0.842	1.33	17.1	0.57
Mean	127.1	50.5	318	7.0	0.56	0.767	1.38	14.3	0.63
S.D.	23.8	3.0	11.5	0.4	0.07	0.06	0.14	1.50	0.07
N2	99.2	47.0	343	13.2	0.73	0.849	2.33	7.1	0.83
N2	143.3	42.6	335	12.5	0.53	0.847	1.90	9.8	0.64
N2	105.3	53.5	358	10.6	0.80	0.829	0.92	8.2	0.88
N2	83.5	48.4	345	12.1	0.57	0.829	2.08	5.9	0.67
N2	98.3	40.2	355	10.3	0.56	0.852	1.60	10.8	0.86
Mean	105.9	46.3	347	11.7	0.64	0.841	1.78	8.4	0.78
S.D.	22.4	5.2	9.3	1.2	0.11	0.01	0.48	1.8	0.10
N3	111.4	40.1	359	23.3	0.56	0.955	1.41	4.9	0.62
N3	137.6	37.1	351	19.9	0.59	0.927	1.65	7.1	0.60
N3	162.8	40.2	322	16.0	0.50	0.775	1.18	7.7	0.82
N3	96.0	41.5	364	12.4	0.68	0.909	1.83	8.0	0.63
N3	140.8	32.1	340	11.8	0.80	0.769	1.71	4.8	0.55
Mean	129.7	38.2	347	16.7	0.63	0.867	1.56	5.8	0.64
S.D.	26.2	3.8	16.8	4.9	0.11	0.08	0.26	1.7	0.09

Conc. (ppm)						Conc. (mg g ⁻¹)
Mn	Al	Zn	Fe	Cu	B	ash
1.57	197	121	64.1	n.d.	n.d.	74
1.52	123	89.9	50.6	2.9	8.0	67
2.34	143	168	64.6	3.5	9.2	95
3.23	132	164	47.9	3.6	12.2	94
3.15	136	161	45.0	3.4	11.6	83
2.36	146	141	54.4	3.4	10.3	83
0.82	29.3	34.2	9.3	0.3	2.0	12.3
1.27	120	34.3	74.2	3.8	6.2	52
1.79	96.0	79.9	48.7	4.7	32.3	58
1.64	150	32.8	45.1	3.5	5.3	47
1.88	131	31.6	46.5	3.5	6.7	55
1.76	102	48.1	45.8	4.2	13.9	55
1.67	120	45.3	52.1	3.9	12.9	53
0.24	21.8	20.4	12.5	0.52	11.4	4.2
1.82	102.0	40.0	41.2	3.5	20.3	51
1.71	86.1	25.4	45.0	3.2	6.5	48
1.35	146.0	29.5	63.2	3.2	4.8	47
1.98	89.2	32.7	37.5	3.7	15.4	48
0.85	164.0	34.9	49.3	2.9	3.6	38
1.54	117.5	32.5	47.2	3.3	10.1	46
0.45	35.4	5.5	9.9	0.31	7.3	4.9
1.67	81.4	85.7	55.9	3.2	12.1	67
2.00	157.0	102.0	41.6	2.8	7.1	70
1.27	143.0	91.4	52.1	2.9	6.8	68
1.90	127.0	80.0	48.0	3.1	5.9	61
2.81	130.0	82.5	47.1	3.4	8.1	77
1.93	127.7	88.3	48.9	3.1	8.0	69
0.51	25.5	7.8	4.8	0.24	2.4	5.8
0.82	117.0	16.9	35.6	3.2	7.1	46
1.64	88.4	56.8	44.5	3.9	20.0	55
0.52	116.0	18.7	44.7	2.7	4.2	46
1.68	139.0	20.9	36.2	2.8	5.6	42
2.00	152.0	58.5	157.0	6.0	17.1	61
1.33	102.5	34.4	63.6	3.7	10.8	50
0.56	48.3	19.1	46.9	1.4	7.2	7.8
1.32	89.5	18.7	47.2	3.5	28.4	35
1.51	89.1	27.7	51.6	3.4	6.4	41
0.88	155.0	22.4	53.7	2.9	5.4	46
1.35	84.4	24.5	32.7	2.8	12.7	46
1.00	126.0	15.8	47.1	2.6	3.8	35
1.21	108.8	21.8	46.5	3.0	11.3	41
0.23	27.5	4.2	7.3	0.4	10.1	5.5